

REGULATORY DYNAMICS ON RANDOM NETWORKS: ASYMPTOTIC PERIODICITY AND MODULARITY

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ABSTRACT. We study the dynamics of discrete-time regulatory networks on random digraphs. For this we define ensembles of deterministic orbits of random regulatory networks, and introduce some statistical indicators related to the long-term dynamics of the system. We prove that, in a random regulatory network, initial conditions converge almost surely to a periodic attractor. We study the subnetworks, which we call modules, where the periodic asymptotic oscillations are concentrated. We prove that those modules are dynamically equivalent to independent regulatory networks.

Keywords: regulatory networks, random graphs, coupled map networks.

1. INTRODUCTION

Numerous natural and artificial systems can be thought as a collection of basic units interacting according to simple rules. Examples of this interacting systems are the genetic regulatory networks, composed of interactions between DNA, RNA, proteins, and small molecules. In social or ecological networks, a similar regulatory dynamics may also be considered. The traditional way to model these systems is by using coupled differential equations, and more particularly systems of piecewise affine differential equations (see [6, 9, 17]). Finite state models, better known as logical networks, are also used (see [11, 13, 19]). Within these modeling strategies, the interacting units have a regular behavior when taken separately, but are capable to generate global complex dynamics when arranged in a complex interaction architecture. In all the models considered so far, each interacting unit regulates some other units in the collection by enhancing or repressing their activity. It is possible then to define an underlying network with interacting units as vertices, and their interactions as arrows connecting those vertices. The theoretical problem we face here is to understand the relation between the structure of the underlying network, and the possible dynamical behaviors of the system. We will do this in the context of a particular class of models first introduced in [22], and further studied

in [5] and [16]. In these models, the level of activity of each unit is codified by a positive real number. The system evolves synchronously at discrete time steps, each unit following an affine contraction dictated by the activity level and interaction mode of its neighboring units. The contraction coefficient of those transformations determines the degradation rate at which, in absence of interactions, the activity of a given unit vanishes. In the framework of this modeling we have proved general results concerning the constraints imposed by the structure of the underlying network, over the possible asymptotic behaviors of a fixed system [16]. In the present paper, following [22], we will focus on the asymptotic dynamics of regulatory systems whose interactions are chosen at random at the beginning of the evolution. Within this approach, individual orbits are elements of a sample space, and the statistical indicators we will study become orbit dependent random variables. The probability measures we used are built from a fixed probability distribution over the set of possible underlying networks. Then, given a fixed underlying network, we associate a sign to each one of its arrows, depending on whether the interaction they represent are activations or inhibitions. Positive and negative signs are randomly chosen, keeping a fixed proportion of negative arrows inside a given statistical ensemble of systems. In this way it is possible to study certain characteristics of the asymptotic dynamics, as function of the degradation rate and the proportion of inhibitory interactions.

Our first result states that in a random regulatory network, initial conditions converge almost surely to a periodic attractor. This result points to the conclusion that in regulatory dynamics, the origin of the complexity is the coexistence of multiple dynamically simple attractors. We prove that this is the case in a full measure set in the parameter space.

According to our preliminary numerical explorations, the long-term oscillations of the system concentrate on subnetwork whose structure depends on the parameters of the statistical ensemble of regulatory networks. Our second result states that the dynamics one can observe when restricted to the oscillatory subnetwork, is equivalent to the dynamics supported by the subnetwork considered as an isolated system. This result allows us to introduce the concept of modularity. If we call module any observable oscillatory subnetwork, then, according to our result, the dynamics of a small network is preserved when it appears as a module in a larger network. We interpret this as the emergence of modularity. This result allows us to predict admissible asymptotic behaviors in regulatory networks admitting disconnected oscillatory subnetworks. It is worth mentioning that this kind of modularity was already studied in the context of Boolean networks [3] and more recently, in continuous-time regulatory networks [10]. Our approach allows a formal approach to the problems addressed in those works.

The paper is organized as follows. In the next section we will introduce the objects under study, then in Section 3 we will state the results, and present some of the proofs. After reviewing two examples, which we do in Section 4, we will give the proofs of the two more technical results in Section 5. The paper ends with a section of final comments and conclusions.

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2. PRELIMINARIES

2.1. Regulatory Networks as Dynamical Systems.

The interaction architecture of the regulatory network is encoded in a directed graph $\mathcal{G} = (V, A)$, where vertices V represent interacting units, and the arrows $A \subset V \times V$ denote interaction between them. To each interaction $(u, v) \in A$ we associate a threshold $T_{(u,v)} \in [0, 1]$, and a sign $\sigma_{(u,v)} \in \{-1, 1\}$ that is chosen according to whether this interaction is an inhibition or an activation. We quantify the activity of each unit $v \in V$ with real number $\mathbf{x}_v \in [0, 1]$. Thus, the activation state of the network at a given time t is determined by the vector $\mathbf{x}^t \in [0, 1]^V$. The influence of a unit u over a target unit v turns on or off, depending on its sign, when the value of \mathbf{x}_u trespasses the threshold $T_{(u,v)}$. The evolution of the network is generated by the iteration of the map $F_{\mathcal{G},\sigma,T,a} : [0, 1]^V \rightarrow [0, 1]^V$ such that

$$(1) \quad \mathbf{x}^{t+1} = F_{\mathcal{G},\sigma,T,a}(\mathbf{x}^t) := a\mathbf{x}^t + (1-a)D_{\mathcal{G},\sigma,T}(\mathbf{x}^t),$$

where the contraction rate $a \in [0, 1)$ determines the speed of degradation of the activity of the units in absence of interaction, and the interaction term $D_{\mathcal{G},\sigma,T} : [0, 1]^V \rightarrow [0, 1]^V$ is the piecewise constant function defined by

$$(2) \quad D_{\mathcal{G},\sigma,T}(\mathbf{x})_v := \frac{1}{\text{Id}(v)} \sum_{u \in V : (u,v) \in A} H(\sigma_{(u,v)} (\mathbf{x}_u - T_{(u,v)})).$$

Here $H : \mathbb{R} \rightarrow \mathbb{R}$ is the Heaviside function, and $\text{Id}(v) := \#\{u \in V : (u, v) \in A\}$ stands for the input degree of the vertex v . We will be referring to the discontinuity set of the transformation $D_{\mathcal{G},\sigma,T}$, which is

$$(3) \quad \Delta_T := \{\mathbf{x} \in [0, 1]^V : \mathbf{x}_u = T_{u,v} \text{ for some } (u, v) \in A\}.$$

For each $a \in [0, 1)$, the transformation $F_{\mathcal{G},\sigma,T,a}$ is a piecewise affine contraction with discontinuity set Δ_T .

From now on, by a discrete-time regulatory network we will mean a discrete-time dynamical system $([0, 1]^V, F_{\mathcal{G},\sigma,T,a})$, with phase space $[0, 1]^V$, and evolution generated by the piecewise affine contraction $F_{\mathcal{G},\sigma,T,a} : [0, 1]^V \rightarrow [0, 1]^V$ defined in Equation (1). The discrete-time regulatory networks studied here have interactions of equal strength, and they act additively on each target unit. More general discrete-time regulatory networks have been considered in [5, 16].

2.2. Statistical Ensembles.

We build our statistical ensembles as follows. We fix the value of the contraction rate $a \in [0, 1)$ and the set V representing the interacting units. Then we consider the set of all possible piecewise transformations,

$$(4) \quad \mathcal{F}_{a,V} := \{F_{\mathcal{G},\sigma,T,a} : \mathcal{G} := (V, A), \sigma \in \{-1, 1\}^A, T \in [0, 1]^A\}.$$

The individual elements of our statistical ensembles are couples $(F_{\mathcal{G},\sigma,T,a}, \mathbf{x})$, with $F_{\mathcal{G},\sigma,T,a} \in \mathcal{F}_{a,V}$ and $\mathbf{x} \in [0, 1]^V$. A couple $(F_{\mathcal{G},\sigma,T,a}, \mathbf{x})$ determines a deterministic orbit $\{\mathbf{x}^t := F_{\mathcal{G},\sigma,T,a}^t(\mathbf{x})\}_{t=0}^\infty$.

We supply the sample space $\mathcal{F}_{a,V} \times [0, 1]^V$ with a probability measure as follows. First we fix a probability distribution \mathbb{P}_G over the set $\mathfrak{G}_V := \{(V, A) : A \subset V \times V\}$ of all directed graphs with vertex set V . Then, for $\eta \in [0, 1]$ and $\mathcal{G} = (V, A)$, we choose sign -1 with probability η and $+1$ with probability $1 - \eta$, independently for each arrow in \mathcal{G} . The thresholds are independent and uniformly distributed random variables in $[0, 1]^A$, as well as the initial conditions in $[0, 1]^V$. In this way we obtain the probability measure $\mathbb{P}_{a,\eta}$ on $\mathcal{F}_{a,V} \times [0, 1]^V$ such that

$$(5) \quad \mathbb{P}_{a,\eta} \{(F_{\mathcal{G},\sigma,T,a}, \mathbf{x}) : T \in \mathcal{I}, \mathbf{x} \in \mathcal{J}\} = \mathbb{P}_G(\mathcal{G}) \times \mathbb{P}_{A,\eta}(\sigma) \times \text{vol}(\mathcal{I}) \times \text{vol}(\mathcal{J}),$$

for all rectangles $\mathcal{I} \subset [0, 1]^A$ and $\mathcal{J} \subset [0, 1]^V$. Here $\mathbb{P}_{A,\eta} : \{-1, 1\}^A \rightarrow [0, 1]$ is such that

$$(6) \quad \mathbb{P}_{A,\eta}(\sigma) = \prod_{(u,v) \in A} \left(\frac{\sigma_{(u,v)} + 1}{2} - \sigma_{(u,v)}\eta \right),$$

and vol stands for the Lebesgue measure on the corresponding euclidean spaces.

2.3. Some graph-theoretical notations and definitions.

A path in $\mathcal{G} = (A, V)$ is a sequence u_0, u_1, \dots, u_k , with $u_i \in V$ and $(u_i, u_{i+1}) \in A$ for each i . The length of a path is the number of arrows it contains. A cycle is a path u_0, u_1, \dots, u_k , where $u_0 = u_k$. We say that the vertices $u, v \in V$ are connected if there exists a cycle u_0, u_1, \dots, u_k such that $u, v \in \{u_0, u_1, \dots, u_k\}$. The connected components of \mathcal{G} are the maximal subgraphs of \mathcal{G} such that all their vertices are connected. The distance between two vertices $u, v \in V$, which we denote $d_{\mathcal{G}}(u, v)$, is the length of the shortest directed path whose end vertices are u and v .

2.4. The oscillatory subnetwork and the asymptotic period.

To each couple $(F_{\mathcal{G},\sigma,T,a}, \mathbf{x})$ we associate a directed graph $\mathcal{G}_{\text{osc}} := (V_{\text{osc}}, A_{\text{osc}}) \subseteq \mathcal{G}$, the oscillatory subnetwork, defined by

$$\begin{aligned} A_{\text{osc}} &:= \{(u, v) \in A : H(\mathbf{x}_u^t - T_{u,v}) \text{ does not converge}\}, \\ V_{\text{osc}} &:= \{v \in V : \exists u \in V \text{ such that } \{(u, v), (v, u)\} \cap A_{\text{osc}} \neq \emptyset\}. \end{aligned}$$

By definition, the oscillatory subnetwork is spanned by all the arrows whose activation state $H(\sigma_{u,v}(\mathbf{x}_u - T_{u,v}))$ changes infinitely often. This subnetwork is the equivalent, in discrete-time regulatory networks, to the dynamical islands introduced in [10] for continuous-time regulatory networks. They are also related to the clusters of relevant elements in Boolean networks, as they were defined in [3]. Unlike the differential equations and the finite state modeling strategies of regulatory dynamics [14, 20, 21], our models admit oscillations in all network topologies, regardless the distribution of activations and inhibitions through the graph. This is possible because of the discreteness of time, and continuity of the state variable. Therefore, oscillatory subnetworks may occur in any discrete-time regulatory network.

The oscillatory subnetwork can be seen as a random variable

$$\mathcal{G}_{\text{osc}} : \mathcal{F}_{a,V} \times [0, 1]^V \rightarrow \mathfrak{G}_{\subseteq V} := \{(\bar{V}, \bar{A}) : \bar{V} \subset V \text{ and } \bar{A} \subset \bar{V} \times \bar{V}\},$$

from which we can derive other statistical indicators, as for instance its size $\#V_{\text{osc}}$, the number $\text{nc}(\mathcal{G}_{\text{osc}})$ of its connected components, and its the degree distribution

$$p_{\mathcal{G}_{\text{osc}}}(k) := \frac{\#\{v \in V_{\text{osc}} : \text{Id}_{\text{osc}}(v) = k\}}{\#V_{\text{osc}}},$$

where $\text{Id}_{\text{osc}}(v) := \{u \in V_{\text{osc}} : (u, v) \in A_{\text{osc}}\}$.

Another statistical indicator we will consider is the asymptotic period of a given orbit. Denote by $\text{Per}_\tau(F_{\mathcal{G},\sigma,T,a})$ the set of all $F_{\mathcal{G},\sigma,T,a}$ -periodic points of minimal period τ , i. e.,

$$(7) \quad \text{Per}_\tau(F_{\mathcal{G},\sigma,T,a}) = \{\mathbf{x} \in [0, 1]^V : F_{\mathcal{G},\sigma,T,a}^\tau(\mathbf{x}) = \mathbf{x} \text{ and } F_{\mathcal{G},\sigma,T,a}^t(\mathbf{x}) \neq \mathbf{x} \text{ if } t < \tau\}.$$

We will say that the asymptotic $F_{\mathcal{G},\sigma,T,a}$ -period of $\mathbf{x} \in [0, 1]^V$ is τ if there exists $\mathbf{y} \in \text{Per}_\tau(F_{\mathcal{G},\sigma,T,a})$, such that

$$\lim_{t \rightarrow \infty} |F_{\mathcal{G},\sigma,T,a}^t(\mathbf{x}) - F_{\mathcal{G},\sigma,T,a}^t(\mathbf{y})| = 0.$$

We will denote this by $P(F_{\mathcal{G},\sigma,T,a}, \mathbf{x}) = \tau$.

3. RESULTS

3.1. The asymptotic period.

To each finite set V , and $a \in [0, 1]$, we associate the sample space $\mathcal{F}_{a,V} \times [0, 1]^V$, with $\mathcal{F}_{a,V}$ as in Equation (4). We supply this sample space with the product sigma-algebra, taking for $[0, 1]^V$ and $[0, 1]^A$, the corresponding Borel sigma-algebras. The next result concerns the asymptotic period $(F_{\mathcal{G},\sigma,T,a}, \mathbf{x}) \mapsto P(F_{\mathcal{G},\sigma,T,a}, \mathbf{x})$.

Theorem 1. *Given a finite set V , and $a \in [0, 1]$, the function $P : \mathcal{F}_{a,V} \times [0, 1]^V \rightarrow \mathbb{N}$ which assigns to $(F_{\mathcal{G},\sigma,T,a}, \mathbf{x}) \in \mathcal{F}_{a,V} \times [0, 1]^V$ the value of the asymptotic $F_{\mathcal{G},\sigma,T,a}$ -period of \mathbf{x} , is a measurable function. Furthermore, for each $\eta \in [0, 1]$,*

$$\mathbb{P}_{a,\eta} \{(F_{\mathcal{G},\sigma,T,a}, \mathbf{x}) \in \mathcal{F}_{a,V} \times [0, 1]^V : P(F_{\mathcal{G},\sigma,T,a}, \mathbf{x}) < \infty\} = 1.$$

This expected but nontrivial result says that a random orbit will almost certainly approach a periodic orbit, otherwise said, an initial condition almost certainly converges to a periodic attractor. It is because of this result that we can restrict ourselves to the study of periodic orbits, even though the parameter set for which the orbits are infinite may be uncountable (see [5]). We could therefore redefine the oscillatory subnetwork by saying that, after a transitory, their arrows change periodically their activation state. The proof of this result and some related comments are left to Subsection 5.1.

3.2. Modularity.

In this paragraph we will consider probability measures obtained by conditioning on a subnetwork, from a given statistical ensemble of regulatory networks. Given $\mathbb{P}_{a,\eta}$ on $\mathcal{F}_{a,V} \times [0,1]^V$, and a subnetwork $\bar{\mathcal{G}} := (\bar{V}, \bar{A}) \in \mathfrak{G}_{\subseteq V}$, we define the analogous probability measure $\mathbb{P}_{a,\eta,\bar{\mathcal{G}}}$ on $\mathcal{F}_{a,\bar{V}} \times [0,1]^{\bar{V}}$, such that

$$(8) \quad \mathbb{P}_{a,\eta,\bar{\mathcal{G}}} \{ (F_{\bar{\mathcal{G}},\bar{\sigma},\bar{T},a}, \mathbf{y}) : \bar{T} \in \bar{\mathcal{I}}, \mathbf{y} \in \bar{\mathcal{J}} \} := \begin{cases} \mathbb{P}_{\bar{A},\eta}(\bar{\sigma}) \text{ vol}(\bar{\mathcal{I}}) \text{ vol}(\bar{\mathcal{J}}) & \text{if } \bar{\mathcal{G}} = \bar{\bar{\mathcal{G}}}, \\ 0 & \text{otherwise,} \end{cases}$$

for each $\bar{\sigma} \in \{-1,1\}^{\bar{A}}$, and all rectangles $\bar{\mathcal{I}} \subset [0,1]^{\bar{A}}$ and $\bar{\mathcal{J}} \subset [0,1]^{\bar{V}}$. As before, vol denotes the corresponding Lebesgue measures. This measure can also be seen as the marginal of $\mathbb{P}_{a,V}$ obtained by projecting over $\bar{V} \subset V$, then conditioned to have underlying network $\bar{\mathcal{G}} \in \mathfrak{G}_{\bar{V}}$.

Theorem 2. *Fix $a \in [0,1)$, $\eta \in [0,1]$, and a digraph $\bar{\mathcal{G}} = (\bar{V}, \bar{A}) \in \mathfrak{G}_{\subseteq V}$ with $\bar{V} \subsetneq V$. If the digraph distribution \mathbb{P}_G is such that $\mathbb{P}_G(\mathcal{G}) > 0$ for all $\mathcal{G} \in \mathfrak{G}_V$, and if $\mathbb{P}_{a,\eta}(\mathcal{G}_{\text{osc}} = \bar{\mathcal{G}}) > 0$, then we can associated to $\bar{\mathcal{G}}$:*

- a) a digraph extension $\bar{\mathcal{G}}_{\text{ext}} := (V, A) \in \mathfrak{G}_V$,
- b) rectangles $\mathcal{I} := \bar{\mathcal{I}} \times \mathcal{I}' \subset [0,1]^{\bar{A}} \times [0,1]^{A \setminus \bar{A}}$ and $\mathcal{J} := \bar{\mathcal{J}} \times \mathcal{J}' \subset [0,1]^{\bar{V}} \times [0,1]^{V \setminus \bar{V}}$,
- c) and for each $\bar{\sigma} \in \{-1,1\}^{\bar{A}}$, an extension $\bar{\sigma}_{\text{ext}} \in \{-1,1\}^A$ such that $\bar{\sigma}_{\text{ext}}|_{\bar{A}} = \bar{\sigma}$.

These associated objects satisfy

$$\mathcal{G}_{\text{osc}}(F_{\bar{\mathcal{G}}_{\text{ext}},\bar{\sigma}_{\text{ext}},T,a}, \mathbf{x}) \subseteq \bar{\mathcal{G}} \quad \forall T \in \mathcal{I}, \mathbf{x} \in \mathcal{J}, \text{ and } \bar{\sigma} \in \{-1,1\}^{\bar{A}}.$$

Furthermore, \mathcal{G}_{ext} , \mathcal{I} , and \mathcal{J} , define surjective transformations

- d) $\Phi_A : \bar{\mathcal{I}} \times \mathcal{I}' \rightarrow [0,1]^A$, such that $\Phi_A(\bar{T} \times T') = \mathcal{D}_{\bar{A}}\bar{T} + \mathcal{C}_{\bar{A}}$ with $\mathcal{D}_{\bar{A}}$ diagonal and $\mathcal{C}_{\bar{A}}$ constant,
- e) and similarly, $\Phi_V : \bar{\mathcal{J}} \times \mathcal{J}' \rightarrow [0,1]^V$ such that $\Phi_V(\bar{\mathbf{x}} \times \mathbf{x}') = \mathcal{D}_{\bar{V}}\bar{\mathbf{x}} + \mathcal{C}_{\bar{V}}$, with $\mathcal{D}_{\bar{V}}$ diagonal and $\mathcal{C}_{\bar{V}}$ constant.

These transformations satisfy

$$\Phi_V \circ F_{\bar{\mathcal{G}},\sigma,T,a}(\mathbf{x}) = F_{\bar{\mathcal{G}},\bar{\sigma},\Phi_A(T),a} \circ \Phi_V(\mathbf{x}),$$

for all $T \in \mathcal{I}$, and $\mathbf{x} \in \mathcal{J}$.

The proof of this result follows from a construction, and it is postponed to Section 5. Let us from now expose its interpretation and some of its consequences. We can divide this Theorem into two parts, the first part concerns the stability of the oscillatory subnetworks. It says that if an oscillatory subnetwork $\bar{\mathcal{G}} := (\bar{V}, \bar{A})$ has positive probability to occur, then to each signs matrix $\bar{\sigma} \in \{-1,1\}^{\bar{A}}$ it corresponds an oscillatory subnetwork which is subgraph of $\bar{\mathcal{G}}$. Furthermore, the set of initial conditions and thresholds for which a given subgraph of $\bar{\mathcal{G}}$ is the oscillatory subnetwork, is a rectangle with nonempty interior. Therefore, each of those subgraphs is stable under small changes in the thresholds $T \in [0,1]^A$, and in the initial condition $\mathbf{x} \in [0,1]^V$. The size of the maximal perturbation depends on the position of (T, \mathbf{x}) with respect to the borders of the above mentioned rectangle.

More interestingly, the second part of the theorem states that if an oscillatory subnetwork has positive probability to occur, then the dynamics one can observe when restricted to that subnetwork is equivalent to the dynamics supported by the subnetwork considered as an isolated system. The equivalence is achieved through the transformation Φ_A and Φ_V . It is because of this equivalence that we can talk about modularity. Indeed, if we call module any oscillatory subnetwork occurring with positive probability, then this theorem can be rephrased by saying that each orbit admissible in a module considered as an isolated system, can be achieved, up to a change of variables, as the restriction of an orbit in the original system. The network extension $\bar{\mathcal{G}}_{\text{ext}}$, the values of the external thresholds $\mathcal{I}' \in [0, 1]^{\bar{A} \setminus A}$, and the external initial conditions $\mathcal{J}' \in [0, 1]^{\bar{V} \setminus V}$, can be thought as the analogous in our systems, to the functionality context defined in [18] for logical networks. Using their nomenclature, our theorem ensures that if an oscillatory subnetwork has a positive probability to occur, then there is positive measure set of contexts making this subnetwork functional.

An interesting consequence of the previous theorem is the following.

Corollary 1. *Fix $a \in [0, 1)$, $\eta \in [0, 1]$, and $\bar{\mathcal{G}} \equiv \mathcal{G}_1 \cup \mathcal{G}_2 \in \mathfrak{G}_{\subseteq V}$, with $\mathcal{G}_1 := (V_1, A_1)$ and $\mathcal{G}_2 := (V_2, A_2)$ vertex disjoint and such that $V_1 \cup V_2 \subsetneq V$. If the digraph distribution \mathbb{P}_G is such that $\mathbb{P}_G(\mathcal{G}) > 0$ for all $G \in \mathfrak{G}_V$, and if $\mathbb{P}_{a,\eta}(\mathcal{G}_{\text{osc}} \subseteq \bar{\mathcal{G}}) > 0$, then*

$$\mathbb{P}_{a,\eta}(P = \tau) \geq C \sum_{\text{lcm}(\tau_1, \tau_2) = \tau} \mathbb{P}_{a,\eta,\mathcal{G}_1}(P = \tau_1) \mathbb{P}_{a,\eta,\mathcal{G}_2}(P = \tau_2),$$

with $C > 0$ a constant depending on $\mathbb{P}_{a,\eta}$ and $\bar{\mathcal{G}}$.

The probabilities in the sum at right hand side of the inequality are analogous probability measures of the kind defined by Equation (8). They are obtained as marginal probability corresponding to projections over vertex the sets V_1 and V_2 , then conditioned to have underlying network \mathcal{G}_1 and \mathcal{G}_2 respectively.

In [3] the authors study the relationship between the modular structure and the periods distribution in Boolean networks. The previous corollary establishes such a relation in the framework of discrete-time regulatory networks. Our result relates the distribution of the asymptotic period of a network \mathcal{G} , to the distribution of the asymptotic period of its oscillatory subnetworks considered as isolated systems. It establishes in particular that the observable asymptotic periods of \mathcal{G} are the least common multiples of the observable asymptotic periods of its oscillatory subnetworks.

Proof. First notice that, for each $\bar{\mathcal{G}} \in \mathfrak{G}_{\subseteq V}$ we have

$$\mathbb{P}_{a,\eta}(P = \tau) \geq \mathbb{P}_{a,\eta}(P = \tau | \mathcal{G}_{\text{osc}} \subseteq \bar{\mathcal{G}}) \times \mathbb{P}_{a,\eta}(\mathcal{G}_{\text{osc}} \subseteq \bar{\mathcal{G}}).$$

Let $\bar{\mathcal{G}} = (\bar{V}, \bar{A}) = (V_1 \cup V_2, A_1 \cup A_2)$, with $\mathcal{G}_1 := (V_1, A_1)$ and $\mathcal{G}_2 := (V_2, A_2)$ vertex disjoint. Theorem 2 ensures the existence of the following objects associate to $\bar{\mathcal{G}}$: a) the extension of $\bar{\mathcal{G}}$, a digraph $\bar{\mathcal{G}}_{\text{ext}} := (V, A) \in \mathfrak{G}_V$ such that $\bar{\mathcal{G}} \subseteq \bar{\mathcal{G}}_{\text{ext}}$, b) two affine surjective transformations

$$\Phi_A : \mathcal{I} \rightarrow [0, 1]^{A_1} \times [0, 1]^{A_2} \text{ and } \Phi_V : \mathcal{J} \rightarrow [0, 1]^{V_1} \times [0, 1]^{V_2},$$

and c) for each $\bar{\sigma} \equiv \bar{\sigma}^{(1)} \times \bar{\sigma}^{(2)} \in \{-1, 1\}^{A_1} \times \{-1, 1\}^{A_2}$, an extension $\bar{\sigma}_{\text{ext}} \in \{-1, 1\}^A$ such that $\sigma|_{A_1 \cup A_2} = \bar{\sigma}$. From the second part of the theorem it follows that

$$(9) \quad \Phi_V \left(F_{\bar{\mathcal{G}}_{\text{ext}}, \bar{\sigma}_{\text{ext}}, T, a}^t(\mathbf{x}) \right) = F_{\mathcal{G}_1, \bar{\sigma}^{(1)}, \bar{T}^{(1)}, a}^t(\mathbf{y}^{(1)}) \times F_{\mathcal{G}_2, \bar{\sigma}^{(2)}, \bar{T}^{(2)}, a}^t(\mathbf{y}^{(2)}),$$

for all $t \in \mathbb{N}$ and $(T, \mathbf{x}) \in \mathcal{I} \times \mathcal{J}$. Here we have used $\Phi_V(T) \equiv \bar{T}^{(1)} \times \bar{T}^{(2)} \in [0, 1]^{A_1} \times [0, 1]^{A_2}$ and $\Phi_V(\mathbf{x}) \equiv \mathbf{y}^{(1)} \times \mathbf{y}^{(2)} \in [0, 1]^{V_1} \times [0, 1]^{V_2}$. For $i = 1, 2$, and each $\bar{\sigma}^{(i)} \in \{-1, 1\}^{A_i}$ and $\tau_i \in \mathbb{N}$, let us define

$$P_{\mathcal{G}_i, \bar{\sigma}^{(i)}, \tau_i} := \left\{ \left(\bar{T}^{(i)}, \mathbf{y}^{(i)} \right) \in [0, 1]^{A_i} \times [0, 1]^{V_i} : P \left(F_{\mathcal{G}_i, \bar{\sigma}^{(i)}, \bar{T}^{(i)}, a}(\mathbf{y}^{(i)}) \right) = \tau_i \right\}.$$

Defining $\Phi : \mathcal{I} \times \mathcal{J} \rightarrow [0, 1]^A \times [0, 1]^V$ such that $\Phi(T, \mathbf{x}) := \Phi_A(T) \times \Phi_V(\mathbf{x})$, it follows from (9) that

$$\begin{aligned} \mathbb{P}_{a, \eta} (P = \tau | \mathcal{G}_{\text{osc}} \subseteq \bar{\mathcal{G}}) &\geq \frac{\mathbb{P}_G(\bar{\mathcal{G}}_{\text{ext}})}{\mathbb{P}_{a, \eta}(\mathcal{G}_{\text{osc}} \subseteq \bar{\mathcal{G}})} \sum_{\bar{\sigma} = \bar{\sigma}^{(1)} \times \bar{\sigma}^{(2)}} \mathbb{P}_{A, \eta}(\bar{\sigma}_{\text{ext}}) \\ &\quad \times \sum_{\text{lcm}(\tau_1, \tau_2) = \tau} \text{vol} \circ \Phi^{-1} \left(P_{\mathcal{G}_1, \bar{\sigma}^{(1)}, \tau_1} \times P_{\mathcal{G}_2, \bar{\sigma}^{(2)}, \tau_2} \right), \end{aligned}$$

where vol denotes Lebesgue measure in $[0, 1]^A \times [0, 1]^V$. Let us now use the decomposition $\mathcal{I} = \bar{\mathcal{I}} \times \mathcal{I}' \subset [0, 1]^{\bar{A}} \times [0, 1]^{A \setminus \bar{A}}$ and $\mathcal{J} = \bar{\mathcal{J}} \times \mathcal{J}' \subset [0, 1]^{\bar{V}} \times [0, 1]^{V \setminus \bar{V}}$. According to Theorem 2, we have

$$\Phi((\bar{T} \times T') \times (\bar{\mathbf{x}} \times \mathbf{x}')) = \mathcal{D}(\bar{T} \times \bar{\mathbf{x}}) + \mathcal{C}$$

where \mathcal{D} is a diagonal linear bijection, and \mathcal{C} is a constant. With this,

$$\begin{aligned} \mathbb{P}_{a, \eta} (P = \tau | \mathcal{G}_{\text{osc}} = \bar{\mathcal{G}}) &\geq \frac{\mathbb{P}_G(\bar{\mathcal{G}}_{\text{ext}}) \text{vol}(\mathcal{I}' \times \mathcal{J}')}{|\mathcal{D}| \mathbb{P}_{a, \eta}(\mathcal{G}_{\text{osc}} \subseteq \bar{\mathcal{G}})} \sum_{\bar{\sigma} = \bar{\sigma}^{(1)} \times \bar{\sigma}^{(2)}} \mathbb{P}_{A, \eta}(\bar{\sigma}_{\text{ext}}) \\ &\quad \times \sum_{\text{lcm}(\tau_1, \tau_2) = \tau} \text{vol}_1 \left(P_{\mathcal{G}_1, \bar{\sigma}^{(1)}, \tau_1} \right) \times \text{vol}_2 \left(P_{\mathcal{G}_2, \bar{\sigma}^{(2)}, \tau_2} \right), \end{aligned}$$

where vol denotes the Lebesgue measure in $[0, 1]^{A \setminus \bar{A}} \times [0, 1]^{V \setminus \bar{V}}$, vol_i denotes the Lebesgue measure in $[0, 1]^{A_i} \times [0, 1]^{V_i}$ for $i = 1, 2$, and $|\mathcal{D}|$ denotes the determinant of the transformation \mathcal{D} . From here, and taking into account the definition in Equation (8), we have

$$\begin{aligned} \mathbb{P}_{a, \eta} (P = \tau | \mathcal{G}_{\text{osc}} = \bar{\mathcal{G}}) &\geq \frac{\mathbb{P}_G(\bar{\mathcal{G}}_{\text{ext}}) \text{vol}(\mathcal{I}' \times \mathcal{J}') \min(\eta, 1 - \eta)^{\#(A \setminus \bar{A})}}{|\mathcal{D}| \mathbb{P}_{a, \eta}(\mathcal{G}_{\text{osc}} \subseteq \bar{\mathcal{G}})} \\ &\quad \times \sum_{\bar{\sigma} = \bar{\sigma}^{(1)} \times \bar{\sigma}^{(2)}} \mathbb{P}_{A_1, \eta}(\bar{\sigma}^{(1)}) \times \mathbb{P}_{A_2, \eta}(\bar{\sigma}^{(2)}) \\ &\quad \times \sum_{\text{lcm}(\tau_1, \tau_2) = \tau} \text{vol}_1 \left(P_{\mathcal{G}_1, \bar{\sigma}^{(1)}, \tau_1} \right) \times \text{vol}_2 \left(P_{\mathcal{G}_2, \bar{\sigma}^{(2)}, \tau_2} \right) \\ &\geq \frac{\mathbb{P}_G(\bar{\mathcal{G}}_{\text{ext}}) \text{vol}(\mathcal{I}' \times \mathcal{J}') \min(\eta, 1 - \eta)^{\#(A \setminus \bar{A})}}{|\mathcal{D}| \mathbb{P}_{a, \eta}(\mathcal{G}_{\text{osc}} \subseteq \bar{\mathcal{G}})} \\ &\quad \times \sum_{\text{lcm}(\tau_1, \tau_2) = \tau} \mathbb{P}_{a, \eta, \mathcal{G}_1}(P = \tau_1) \mathbb{P}_{a, \eta, \mathcal{G}_2}(P = \tau_2), \end{aligned}$$

and the result follows with $C := \mathbb{P}_G(\bar{\mathcal{G}}_{\text{ext}}) \times \text{vol}(\mathcal{I}' \times \mathcal{J}') \times \min(\eta, 1 - \eta)^{\#(A \setminus \bar{A})} / |\mathcal{D}|$. \square

3.3. Sign Symmetry.

The next result illustrates how a structural constrain in the underlying random network manifests in the distribution of the statistical indicators. Here, the fact that the underlying random digraph does not admit cycles of odd length, implies a symmetry on the statistical indicators with respect to the change of sign in the interactions. Let us remind that for each $\eta \in [0, 1]$ and $a \in [0, 1)$, the probability measure $\mathbb{P}_{a,\eta}$ on $\mathcal{F}_{a,V} \times [0, 1]^V$ which defines a statistical ensemble, is obtained from a fixed distribution \mathbb{P}_G over the finite set of all directed graphs with vertices in V . We have the following.

Proposition 1. *If the distribution \mathbb{P}_G over the set \mathfrak{G}_V of all directed graphs with vertices in V is such that $\mathbb{P}_G\{\mathcal{G} \in \mathfrak{G}_V : \mathcal{G} \text{ admits a cycle of odd length}\} = 0$, then*

$$\begin{aligned} \mathbb{P}_{a,\eta}(P = \tau) &= \mathbb{P}_{a,1-\eta}(P = \tau), \quad \forall \tau \in \mathbb{N}, \\ \mathbb{P}_{a,\eta}(\mathcal{G}_{\text{osc}} = \bar{\mathcal{G}}) &= \mathbb{P}_{a,1-\eta}(\mathcal{G}_{\text{osc}} = \bar{\mathcal{G}}) \quad \forall \bar{\mathcal{G}} \in \mathfrak{G}_{\subseteq V}, \end{aligned}$$

for each $\eta \in [0, 1]$.

Statistical ensembles of regulatory networks whose underlying digraphs are random trees (as defined in Subsection 4.1 below) clearly satisfy the hypothesis of Proposition 1. Random subnetworks of the square lattice also have this property. Therefore, for regulatory dynamics over those kind of digraphs, the statistical indicators we consider are left invariant under the symmetry $\eta \mapsto 1 - \eta$.

In the proof of Proposition 1, we will need the following.

Lemma 1. *For each $\mathcal{G} := (V, A) \in \mathfrak{G}_V$, and $\sigma \in \{-1, 1\}^V$ we have,*

$$\text{vol}\{(T, \mathbf{x}) \in [0, 1]^A \times [0, 1]^V : \{F_{\mathcal{G}, \sigma, T, a}^t(\mathbf{x}) : t \in \mathbb{N}\} \cap \Delta_T = \emptyset\} = 1.$$

where $\Delta_T := \{\mathbf{x} \in [0, 1]^V : \mathbf{x}_u = T_{u,v} \text{ for some } (u, v) \in A\}$ is the discontinuity set of the piecewise constant part of $F_{\mathcal{G}, \sigma, T, a}$.

This lemma directly follows from the arguments developed below, in paragraphs 5.1.3 and 5.1.4, inside the proof of Theorem 1.

Proof of Proposition 1. First notice that, for each $\mathcal{G} = (A, V) \in \mathfrak{G}_V$ and $\sigma \in \{-1, 1\}^A$ we have

$$\begin{aligned} \mathbb{P}_{A,1-\eta}(-\sigma) &= \prod_{(u,v) \in A} \left(\frac{-\sigma_{(u,v)} + 1}{2} + \sigma_{(u,v)}(1 - \eta) \right) \\ &= \prod_{(u,v) \in A} \left(\frac{\sigma_{(u,v)} + 1}{2} - \sigma_{(u,v)}\eta \right) = \mathbb{P}_{A,\eta}(\sigma). \end{aligned}$$

Let us suppose that all the cycles in \mathcal{G} have even length, and for each connected component of $\bar{\mathcal{G}} := (\bar{A}, \bar{V}) \subseteq \mathcal{G} = (A, V) \in \mathfrak{G}_V$, choose a pivot vertex $\bar{u} \in \bar{V}$. With this define

$\Psi_A : [0, 1]^A \rightarrow [0, 1]^A$ and $\Psi_V : [0, 1]^V \rightarrow [0, 1]^V$ such that

$$\Psi_A(T)_{(u,v)} := \begin{cases} 1 - T_{(u,v)} & \text{if } d_{\mathcal{G}}(u, \bar{u}) \in 2\mathbb{N} \\ T_{(u,v)} & \text{otherwise} \end{cases} \quad \Psi_V(\mathbf{x})_u := \begin{cases} 1 - \mathbf{x}_u & \text{if } d_{\mathcal{G}}(u, \bar{u}) \in 2\mathbb{N} \\ \mathbf{x}_u & \text{otherwise,} \end{cases}$$

for each $u, v \in \bar{V}$. Here $d_{\mathcal{G}}$ denotes vertex distance induced by the digraph \mathcal{G} , as defined in Subsection 2.3. Both Ψ_A and Ψ_V are affine isometries, therefore they preserve the Lebesgue measure in $[0, 1]^A$ and $[0, 1]^V$ respectively. If $d_{\mathcal{G}}(v, \bar{u})$ is even, then $\Psi_V(\mathbf{x})_v = 1 - \mathbf{x}_v$, and for each u such that $(u, v) \in A$, $\Psi_V(\mathbf{x})_u = \mathbf{x}_u$ and $\Psi_A(T)_{(u,v)} = T_{(u,v)}$. In this case we have

$$\begin{aligned} F_{\mathcal{G}, -\sigma, \Psi_A(T), a}(\Psi_V(\mathbf{x}))_v &= a(1 - \mathbf{x}_v) + \frac{1-a}{\text{Id}(v)} \sum_{u \in V: (u,v) \in A} H(-\sigma_{(u,v)}(\mathbf{x}_u - T_{(u,v)})) \\ &= a(1 - \mathbf{x}_v) + \frac{1-a}{\text{Id}(v)} \sum_{u \in V: (u,v) \in A} (1 - H(\sigma_{(u,v)}(\mathbf{x}_u - T_{(u,v)}))) \\ &= 1 - F_{\mathcal{G}, \sigma, T, a}(\mathbf{x})_v = \Psi_V(F_{\mathcal{G}, \sigma, T, a}(\mathbf{x}))_v, \end{aligned}$$

for each $\mathbf{x} \notin \Delta_T$. On the other hand, if $d_{\mathcal{G}}(v, v_{\text{pivot}})$ is odd, we have $\Psi_V(\mathbf{x})_v = \mathbf{x}_v$, and for each u such that $(u, v) \in A$, $\Psi_V(\mathbf{x})_u = 1 - \mathbf{x}_u$ and $\Psi_A(T)_{(u,v)} = 1 - T_{(u,v)}$. In this case

$$\begin{aligned} F_{\mathcal{G}, -\sigma, \Psi_A(T), a}(\Psi_V(\mathbf{x}))_v &= a\mathbf{x}_v + \frac{1-a}{\text{Id}(v)} \sum_{u \in V: (u,v) \in A} H(-\sigma_{(u,v)}((1 - \mathbf{x}_u) - (1 - T_{(u,v)}))) \\ &= a\mathbf{x}_v + \frac{1-a}{\text{Id}(v)} \sum_{u \in V: (u,v) \in A} H(\sigma_{(u,v)}(\mathbf{x}_u - T_{(u,v)})) \\ &= F_{\mathcal{G}, \sigma, T, a}(\mathbf{x})_v = \Psi_V(F_{\mathcal{G}, \sigma, T, a}(\mathbf{x}))_v, \end{aligned}$$

for each $\mathbf{x} \notin \Delta_T$. Taking into account Lemma 1, $F_{\mathcal{G}, -\sigma, \Psi_A(T), a}^t(\Psi_V(\mathbf{x})) = \Psi_V(F_{\mathcal{G}, \sigma, T, a}^t(\mathbf{x}))$ for all $t \in \mathbb{N}$, for almost all $(\mathbf{x}, T) \in [0, 1]^A \times [0, 1]^V$. Since Φ_V is an isometry, we immediately have

$$\text{vol} \{ (T, \mathbf{x}) \in [0, 1]^A \times [0, 1]^A : P(F_{\mathcal{G}, -\sigma, \Psi_A(T), a}, \Psi_V(\mathbf{x})) = P(F_{\mathcal{G}, \sigma, T, a}, \mathbf{x}) \} = 1,$$

for all $\mathcal{G} := (V, A) \in \mathfrak{G}_V$ with no odd cycles, and every $\sigma \in \{-1, 1\}^A$. Since both Ψ_A and Ψ_V preserve the respective Lebesgue measure, and $\mathbb{P}_G(\mathfrak{G} \text{ admits an odd cycle}) = 0$, we obtain

$$\begin{aligned} \mathbb{P}_{a, \eta}(P = \tau) &= \sum_{\mathcal{G} \in \mathfrak{G}_V} \mathbb{P}_G(\mathcal{G}) \sum_{\sigma \in \{-1, 1\}^A} \mathbb{P}_{A, 1-\eta}(-\sigma) \\ &\quad \times \text{vol} \{ (T, \mathbf{x}) : P(F_{\mathcal{G}, -\sigma, \Psi_A(T), a}, \Psi_V(\mathbf{x})) = \tau \} \\ &= \sum_{\mathcal{G} \in \mathfrak{G}_V} \mathbb{P}_G(\mathcal{G}) \sum_{\sigma \in \{-1, 1\}^A} \mathbb{P}_{A, 1-\eta}(-\sigma) \text{vol} \{ (T, \mathbf{x}) : P(F_{\mathcal{G}, -\sigma, T, a}, \mathbf{x}) = \tau \} \\ &= \mathbb{P}_{a, 1-\eta}(P = \tau), \end{aligned}$$

for all $\tau \in \mathbb{N}$, and this concludes the proof of the first claim in the proposition.

For the second claim, if $F_{\mathcal{G},\sigma,T,a}^t(\mathbf{x}) \notin \Delta_T$, then

$$\begin{aligned} H(\sigma_{(u,v)}(F_{\mathcal{G},\sigma,T,a}^t(\mathbf{x})_u - T_{(u,v)})) &= H(-\sigma_{u,v}(\Psi_V(F_{\mathcal{G},\sigma,T,a}^t(\mathbf{x}))_u - \Psi_A(T)_{(u,v)})) \\ &= H(-\sigma_{u,v}(F_{\mathcal{G},-\sigma,\Psi_A(T),a}^t(\Psi_V(\mathbf{x}))_u - \Psi_A(T)_{(u,v)})). \end{aligned}$$

Therefore, by Lemma 1,

$$\text{vol}\{(T, \mathbf{x}) \in [0, 1]^A \times [0, 1]^A : \mathcal{G}_{\text{osc}}(F_{\mathcal{G},-\sigma,\Psi_A(T),a}, \Psi_V(\mathbf{x})) = \mathcal{G}_{\text{osc}}(F_{\mathcal{G},\sigma,T,a}, \mathbf{x})\} = 1,$$

for all $\mathcal{G} := (V, A) \in \mathfrak{G}_V$ all of whose cycles have even length, and every $\sigma \in \{-1, 1\}^A$. From here, taking into account that $\mathbb{P}_G(\mathcal{G} \text{ admits an odd cycle}) = 0$, and the fact that that Ψ_A and Ψ_V preserve the Lebesgue measure, we obtain

$$\begin{aligned} \mathbb{P}_{a,\eta}(\mathcal{G}_{\text{osc}} = \bar{\mathcal{G}}) &= \sum_{\mathcal{G} \in \mathfrak{G}_V} \mathbb{P}_G(\mathcal{G}) \sum_{\sigma \in \{-1, 1\}^A} \mathbb{P}_{A,1-\eta}(-\sigma) \\ &\quad \times \text{vol}\{(T, \mathbf{x}) : \mathcal{G}_{\text{osc}}(F_{\mathcal{G},-\sigma,\Psi_A(T),a}, \Psi_V(\mathbf{x})) = \bar{\mathcal{G}}\} \\ &= \sum_{\mathcal{G} \in \mathfrak{G}_V} \mathbb{P}_G(\mathcal{G}) \sum_{\sigma \in \{-1, 1\}^A} \mathbb{P}_{A,1-\eta}(-\sigma) \text{vol}\{(T, \mathbf{x}) : \mathcal{G}_{\text{osc}}(F_{\mathcal{G},-\sigma,T,a}, \mathbf{x}) = \bar{\mathcal{G}}\} \\ &= \mathbb{P}_{a,1-\eta}(\mathcal{G}_{\text{osc}} = \bar{\mathcal{G}}), \end{aligned}$$

for all $\bar{\mathcal{G}} \in \mathfrak{G}_{\subseteq V}$, and the proof is completed. \square

4. EXAMPLES

In this section we present, as a matter of illustration, two families of random digraphs which we have explored numerically. A detailed numerical study, which requires massive calculations, is out of the purpose of the present work, and is left for a future research. Instead, in this section we make some general observations suggested by a preliminary numerical exploration of these examples.

4.1. Two Families of Random digraphs.

We consider two kind of distributions \mathbb{P}_G on the set $\mathfrak{G}_V := \{(V, A) : A \subset V \times V\}$ of all directed graph with vertex set V . On one hand we have a directed version of the classical Erdős–Rényi ensemble, which we define as follows.

Fix a vertex set V and $p \in (0, 1)$, and consider the probability distribution $\mathbb{P}_p : \mathfrak{G}_V \rightarrow [0, 1]$ such that $\mathbb{P}_p(A) = p^{\#A}$. According to this, a directed graph contains the arrow (u, v) with probability p , and the inclusion of different vertices are independent and identically distributed random variables. The typical Erdős–Rényi graph is statistically homogeneous, thus suited for a mean field treatment. Most of the rigorous results concerning random graphs refer to these kind of models (see [4, 8] and references therein).

The other family of random digraphs we will refer to derives from the famous Barabási–Albert model of scale-free random graphs, whose popularity relies on the ubiquity of the scale-free property [2, 15]. A dynamical construction of scale-free graphs was proposed

by Barabási and Albert in [1] (see [8] for a more rigorous presentation). Their model incorporates two key ingredients: continuous growth and preferential attachment. We implemented their construction as follows. For $n = 0$, we take $\mathcal{G}_0 = K_{m_0}$, the complete simple undirected graph in m_0 vertices. Then, for each $n \geq 1$, a new vertex v_{n+1} is added to the graph $\mathcal{G}_n := (E_n, V_n)$. This new vertex forms new edges with randomly chosen vertices in V_n . The probability for $v \in V_n$ to be chosen is proportional to its degree in \mathcal{G}_0 , i. e.,

$$\{v_{n+1}, v\} \in E_n \text{ with probability } p_n(v) := \frac{\#\{u \in V_n : \{u, v\} \in E_n\}}{\#E_n}.$$

At the $(n + 1)$ -th step we obtain a graph \mathcal{G}_{n+1} with an increased vertex set $V_{n+1} := V_n \cup \{v_{n+1}\}$ and an enlarged edge set E_{n+1} . This random iteration continues until a predetermined number N of vertices is obtained. In this scheme we are able to add more than one edge at each iteration. If on the contrary, we allow only one new edge at each time step, and we start with $m_0 = 2$ vertices choosing at the 1-th step one of the two preexisting vertices to form a new edge with probability $1/2$, then the resulting graph would be a random scale-free tree [8]. In any case, the final graph \mathcal{G}_{N-m_0} is turned into a directed graph $\mathcal{G} = (V, A)$ by randomly assigning a direction to each edge $\{u, v\} \in E_{N-m_0}$. In our case we choose one of the two possible directions with probability $1/4$, and give probability $1/2$ to the choice of both directions. This procedure generates a probability distribution \mathbb{P}_{BA} in $\mathfrak{G}_V := \{(V, A) : A \subset V \times V\}$.

4.2. Erdoš–Rényi.

We generated random digraphs of the Erdoš–Rényi kind with 100 vertices, and probability of connection $p \in \{0.2, 0.4, 0.6, 0.8\}$. For p fixed and each $\eta \in \{0, 0.1, 0.2, \dots, 1\}$, we build 20 graphs, to which we randomly and uniformly assign thresholds, and signs with probability $\mathbb{P}_{A, \eta}$. By taking $a \in \{0.0, 0.1, 0.2, \dots, 0.8\}$, we obtain 7920 regulatory networks, 20 for each triplet $(p, a, \eta) \in \{0.2, 0.4, 0.6, 0.8\} \times \{0.0, 0.1, \dots, 0.8\} \times \{0, 0.1, 0.2, \dots, 1\}$. Finally, for each one of those dynamical systems we run 30 initial conditions randomly taken from $[0, 1]^{100}$, and we let the system evolve in order to determine the corresponding oscillatory subnetwork and the asymptotic period.

The characteristics of the oscillatory subnetwork depend strongly on the parameter a , and less noticeably on η . We have observed that the mean size of the oscillatory subnetwork decreases with a in a seemingly monotonous way, and does not appear to depend on η . The mean number of connected components never exceeded 2. A crude inspection of the degree distributions of the oscillatory subnetworks suggests that they form an ensemble of the Erdoš–Rényi type, nevertheless, any conclusion in this direction requires a more detailed numerical study. Finally, the mean value of the asymptotic period seems to grow with both a and η . It increases monotonously with a , while for each fixed a , it reaches a local maximum around $\eta = 0.5$.

As a matter of illustration, in Figure 1 we show two digraph with vertex set $V = \{1, 2, \dots, 50\}$. At the left side we draw a random digraph $\mathcal{G} \in \mathfrak{G}_V$ according to the distribution \mathbb{P}_p , with $p = 0.1$. The signs of the arrows correspond to a random choice according to $\mathbb{P}_{A, \eta}$, with $\eta = 0.5$, i. e., both signs have the same probability to be chosen. The digraph at right is the oscillatory subnetwork $\bar{\mathcal{G}} = \mathcal{G}_{\text{osc}}(F_{\mathcal{G}, \sigma, T, a}, \mathbf{x})$, corresponding to

a certain choice of thresholds $T \in [0, 1]^A$ and initial condition $\mathbf{x} \in [0, 1]^V$. The contraction rate was $a = 0.2$. In the oscillatory subnetwork, the direction of an arrow (u, v) is indicated by marking head v with a \times sign.

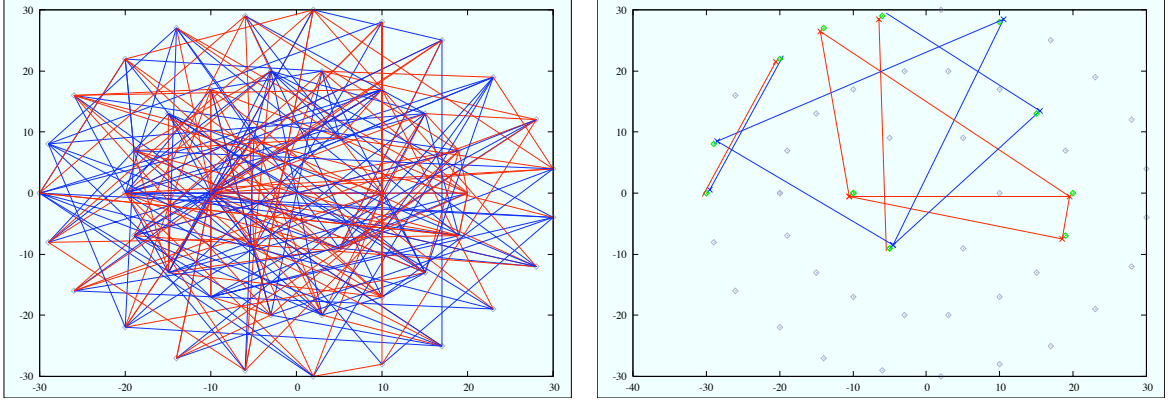


FIGURE 1. An Erdős-Rényi network and corresponding oscillatory subnetwork. The underlying graph was built with a connection probability $p = 0.1$, and the oscillatory subnetwork corresponds to a random initial condition, with random threshold values, and contraction rate $a = 0.2$. Signs are codified by colors: blue for $+1$, and red for -1 . They appear with equal probability $\eta = 0.5$. In the oscillatory subnetwork, the direction of an arrow is indicated by marking its head vertex with a \times .

4.3. Barabási-Albert.

Following the procedure described in 4.1 we generate, starting from a complete graph in $m_0 = 5$ vertices, ensembles of random digraphs of the Barabási-Albert kind of size $N = 100$. For each $\eta \in \{0, 0.1, 0.2, \dots, 1\}$, we generate 20 random graphs, then we turn them into directed graphs by choosing one of the two possible directions with probability $1/4$, and both directions with probability $1/2$. Finally we randomly assign thresholds, and signs with probability $\mathbb{P}_{A,\eta}$, to each one of the 20 resulting digraphs. By ranging $a \in \{0.0, 0.2, 0.4, 0.6\}$, we obtain 880 regulatory networks, 20 for each couple $(a, \eta) \in \{0.0, 0.2, 0.4, 0.6\} \times \{0, 0.1, 0.2, \dots, 1\}$. Then, for each one of those dynamical systems, we randomly select 30 initial conditions in $[0, 1]^{100}$, and let the system evolve in order to determine the corresponding oscillatory subnetwork and the asymptotic period.

For this family of random networks, the mean size of the oscillatory subnetwork behaves in a similar way as for the Erdős-Rényi family, i. e., it increases nonmonotonously with η , with a local maximum at $\eta = 0.5$, and decreases monotonously with a . The mean number of connected components (ranging from 0 to 10) shows a similar behavior with respect to both η and a , with a very noticeable increase around $\eta = 0.5$. On the other hand, the distribution of the asymptotic period becomes broader as we approach $\eta = 0.5$, and for each value of η , the mean value of the asymptotic period grows with a . It is worth to notice that these distributions become broader as a increases, and at the same time the

number of connected components grows. This behavior is consistent with the proliferation of periods predicted by Corollary 1, in the case of a statistical ensemble whose oscillatory subnetworks have many connected components.

In Figure 2 we show two digraph with vertex set $V = \{1, 2, \dots, 50\}$. At the left side we draw a random digraph $\mathcal{G} \in \mathfrak{G}_V$ according to the distribution \mathbb{P}_{BA} . The sign of the arrows is randomly chosen by using the distribution $\mathbb{P}_{A,\eta}$ with $\eta = 0.5$, i. e., both signs have the same probability. The digraph at right is the oscillatory subnetwork $\bar{\mathcal{G}} = \mathcal{G}_{\text{osc}}(F_{\mathcal{G},\sigma,T,a}, \mathbf{x})$, determined by a random choice of thresholds $T \in [0, 1]^A$ and initial condition $\mathbf{x} \in [0, 1]^V$, with contraction rate $a = 0.2$. In the oscillatory subnetwork, the direction of the arrows is indicated by marking the head with a \times .

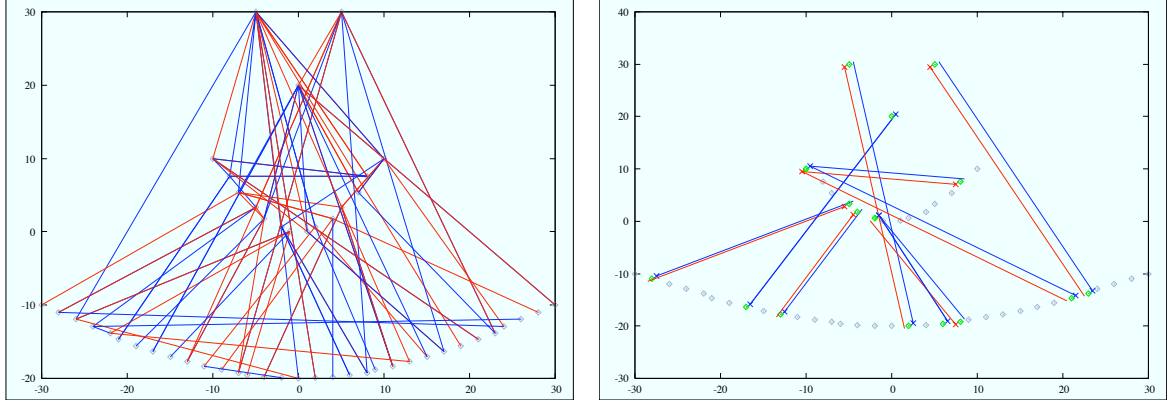


FIGURE 2. A Barabási–Albert network and corresponding oscillatory subnetwork. The underlying graph was built according to the procedure described in Paragraph 4.1, starting with $m_0 = 3$ vertices. The oscillatory subnetwork corresponds to a random initial condition, with random threshold values, and contraction rate $a = 0.2$. Signs are codified by colors: blue for $+1$, and red for -1 . They appear with equal probability $\eta = 0.5$. In the oscillatory subnetwork, the direction of the arrows is indicated by marking the head with a \times .

In Figure 3 we show the behavior of the probability to approach a fixed point, and the probability for the asymptotic period to be equals 2, both as a function of a and η . This picture summarizes the statistics of the 26400 orbits generated on Barabási–Albert like networks, and presents the symmetry $\eta \rightarrow 1 - \eta$ predicted by Proposition 1. This symmetry is expected in an ensemble of regulatory network whose underlying digraphs have no odd length cycles. Though the underlying networks of the experiments we performed have both odd and even length cycles, there is a larger proportion of even lengths amongst the cycles of small length.

5. PROOFS

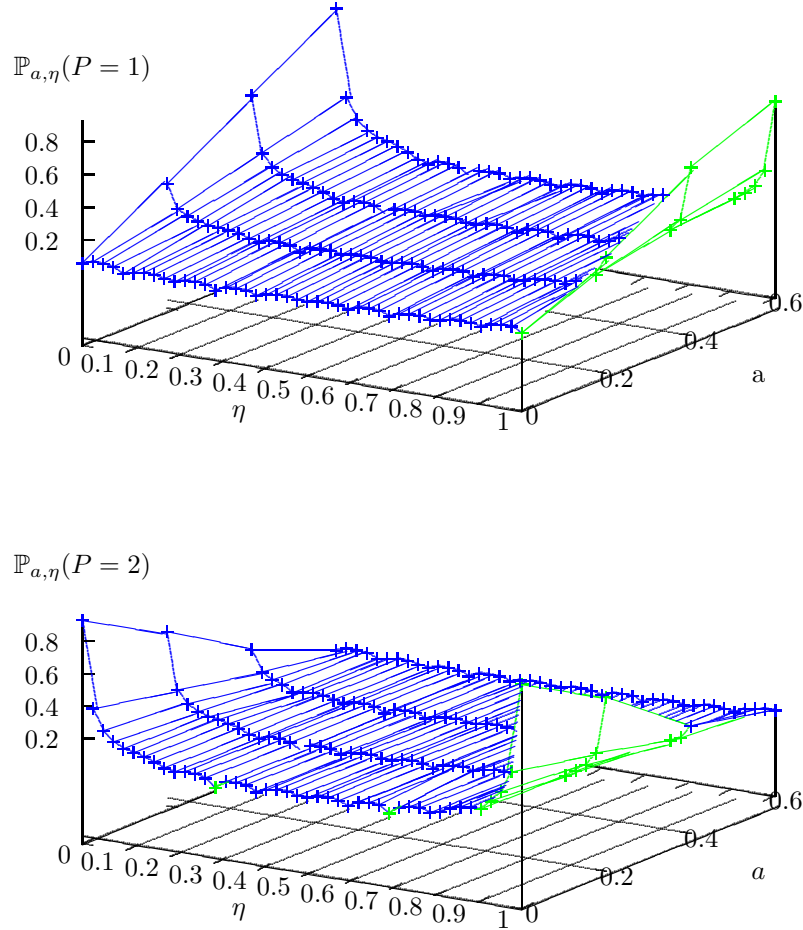


FIGURE 3. At the top, the probability to approach a fixed point in the Barabási–Albert ensembles, as a function of a and η . At the bottom, the probability for the asymptotic period to be equals 2, also as a function of a and η , for the same ensembles.

5.1. Proof of Theorem 1.

Given $\mathcal{G} = (V, A)$, we will use the distance $d_{\max}(\mathbf{x}, \mathbf{y}) := \max_i |\mathbf{x}_i - \mathbf{y}_i|$ in both $[0, 1]^V$ and $[0, 1]^A$. As usual, $d_{\max}(\mathbf{x}, E) := \inf\{d_{\max}(\mathbf{x}, \mathbf{y}) : \mathbf{y} \in E\}$ for $\mathbf{x} \in [0, 1]^F$ and $E \subset [0, 1]^F$. First notice that for \mathcal{G}, σ and a fixed, the set

$$(10) \quad O_{\mathcal{G}, \sigma, a} := \left\{ (T, \mathbf{x}) \in [0, 1]^A \times [0, 1]^V : \inf_{t \geq 0} d_{\max}(F_{\mathcal{G}, \sigma, T, a}^t(\mathbf{x}), \Delta_T) > 0 \right\}$$

is open. Indeed, if $(T, \mathbf{x}) \in O_{\mathcal{G}, \sigma, a}$, then $d_{\max}(F_{\mathcal{G}, \sigma, T, a}^t(\mathbf{x}), \Delta_T) > 3\varepsilon$, for some $\varepsilon > 0$ and all $t \geq 0$. The orbit does not change if we perturb T , i. e., for each $T' \in B_\varepsilon(T)$ we have

$F_{\mathcal{G},\sigma,T',a}^t(\mathbf{x}) = F_{\mathcal{G},\sigma,T,a}^t(\mathbf{x})$ for all $t \in \mathbb{N}$. Furthermore, since $d_{\max}(F_{\mathcal{G},\sigma,T',a}^t(\mathbf{x}), \Delta_{T'}) > 2\varepsilon$, then $d_{\max}(F_{\mathcal{G},\sigma,T',a}^t(\mathbf{y}), \Delta_{T'}) > \varepsilon$ for all $\mathbf{y} \in B_\varepsilon(\mathbf{x})$, therefore $B_\varepsilon(T) \times B_\varepsilon(\mathbf{x}) \subset O_{\mathcal{G},\sigma,a}$.

Since for each \mathcal{G}, σ and a fixed, the set $O_{\mathcal{G},\sigma,a}$ is open in $[0, 1]^A \times [0, 1]^V$, then

$$(11) \quad O_{a,V} := \bigcup_{\mathcal{G}} \bigcup_{\sigma \in \{-1,1\}^A} \bigcup \{(F_{\mathcal{G},\sigma,T,a}, \mathbf{x}) : (T, \mathbf{x}) \in O_{\mathcal{G},\sigma,a}\}$$

is measurable in $\mathcal{F}_{a,V} \times [0, 1]^V$.

5.1.1. *The asymptotic period is measurable in $O_{a,V}$.*

Fix \mathcal{G}, σ and a , and take $(T, \mathbf{x}) \in O_{\mathcal{G},\sigma,a}$ such that $P(F_{\mathcal{G},\sigma,T,a}, \mathbf{x}) = \tau$. There exists $\hat{\mathbf{y}} \in \text{Per}_\tau(F_{\mathcal{G},\sigma,T,a})$ and $N \in \mathbb{N}$, such that

$$d_{\max}(F_{\mathcal{G},\sigma,T,a}^N(\mathbf{x}), \hat{\mathbf{y}}) < \varepsilon := \frac{\inf_{t \geq 0} d_{\max}(F_{\mathcal{G},\sigma,T,a}^t(\mathbf{x}), \Delta_T)}{3}.$$

Hence, for each $t \geq 0$ we have $d_{\max}(F_{\mathcal{G},\sigma,T,a}^{N+t}(\mathbf{x}), F_{\mathcal{G},\sigma,T,a}^t(\hat{\mathbf{y}})) < a^t \varepsilon$. By the same argument as in the previous paragraph, $d_{\max}(F_{\mathcal{G},\sigma,T',a}^{N+t}(\mathbf{y}), F_{\mathcal{G},\sigma,T',a}^t(\hat{\mathbf{y}})) < a^t \varepsilon + a^{N+t} \varepsilon < 2a^t \varepsilon$ for all $t \geq 0$. Therefore $P(F_{\mathcal{G},\sigma,T',a}, \mathbf{y}) = \tau$ for all $(T', \mathbf{y}) \in B_\varepsilon(T) \times B_\varepsilon(\mathbf{x})$. In this way we have proved that for each \mathcal{G}, σ and a fixed, the set

$$O_{\mathcal{G},\sigma,a}^{(\tau)} := \{(T, \mathbf{x}) \in [0, 1]^A \times [0, 1]^V : P(F_{\mathcal{G},\sigma,T,a}, \mathbf{x}) = \tau\}$$

is an open set in $[0, 1]^A \times [0, 1]^V$, therefore

$$P^{-1}\{\tau\} \cap O_{a,V} := \bigcup_{\mathcal{G}} \bigcup_{\sigma \in \{-1,1\}^A} \bigcup \{(F_{\mathcal{G},\sigma,T,a}, \mathbf{x}) : (T, \mathbf{x}) \in O_{\mathcal{G},\sigma,a}^{(\tau)}\}$$

is measurable in $\mathcal{F}_{a,V} \times [0, 1]^V$.

5.1.2. *The asymptotic period is finite in $O_{a,V}$.*

For $(F_{\mathcal{G},\sigma,T,a}, \mathbf{x}) \in O_{a,V}$ let $\hat{\mathbf{x}} \in \text{closure}(\{F_{\mathcal{G},\sigma,T,a}^t(\mathbf{x}) : t \in \mathbb{N}\}_{t \in \mathbb{N}})$ be such that

$$\inf_{t \geq 0} d_{\max}(F_{\mathcal{G},\sigma,T,a}^t(\mathbf{x}), \Delta_T) = d_{\max}(\hat{\mathbf{x}}, \Delta_T) = \varepsilon > 0.$$

Notice that $(F_{\mathcal{G},\sigma,T,a}, \hat{\mathbf{x}}) \in O_{a,V}$ too, and $\inf_{t \geq 0} d_{\max}(F_{\mathcal{G},\sigma,T,a}^t(\hat{\mathbf{x}}), \Delta_T) = d_{\max}(\hat{\mathbf{x}}, \Delta_T) = \varepsilon$.

For $N \in \mathbb{N}$ such that $d_{\max}(F_{\mathcal{G},\sigma,T,a}^N(\mathbf{x}), \hat{\mathbf{x}}) < \varepsilon$ we have $d_{\max}(F_{\mathcal{G},\sigma,T,a}^{N+t}(\mathbf{x}), F^t(\hat{\mathbf{x}})) \leq a^t \varepsilon$ for all $t \geq 0$. Now, for $\tau \in \mathbb{N}$ such that $a^\tau < 1/4$ and $d_{\max}(F_{\mathcal{G},\sigma,T,a}^{N+\tau}(\mathbf{x}), \hat{\mathbf{x}}) < \varepsilon/4$, we have

$$\begin{aligned} d_{\max}(F_{\mathcal{G},\sigma,T,a}^\tau(\hat{\mathbf{x}}), \hat{\mathbf{x}}) &\leq d_{\max}(F_{\mathcal{G},\sigma,T,a}^{N+\tau}(\mathbf{x}), \hat{\mathbf{x}}) + d_{\max}(F_{\mathcal{G},\sigma,T,a}^{N+\tau}(\mathbf{x}), F^\tau(\hat{\mathbf{x}})) \\ &< \varepsilon/4 + a^\tau \varepsilon < \varepsilon/2. \end{aligned}$$

Since $\inf_{t \geq 0} d_{\max} \left(F_{\mathcal{G}, \sigma, T, a}^t(\hat{\mathbf{x}}), \Delta_T \right) = \varepsilon$, then

$$d_{\max} \left(F_{\mathcal{G}, \sigma, T, a}^{k\tau}(\hat{\mathbf{x}}), F_{\mathcal{G}, \sigma, T, a}^{(k-1)\tau}(\hat{\mathbf{x}}) \right) < \frac{a^{(k-1)\tau} \varepsilon}{2} < \frac{\varepsilon}{2^{2k-1}},$$

for all $k \in \mathbb{N}$. Hence $\hat{\mathbf{y}} := \lim_{k \rightarrow \infty} F_{\mathcal{G}, \sigma, T, a}^{k\tau}(\hat{\mathbf{x}})$ exists and satisfies $F_{\mathcal{G}, \sigma, T, a}^\tau(\hat{\mathbf{y}}) = \hat{\mathbf{y}}$. Furthermore, since $d_{\max}(\hat{\mathbf{x}}, \hat{\mathbf{y}}) < \varepsilon \sum_{k=1}^{\infty} 2^{1-2k} = 2\varepsilon/3$, then

$$d_{\max} \left(F_{\mathcal{G}, \sigma, T, a}^{N+k\tau}(\mathbf{x}), \hat{\mathbf{y}} \right) \leq d_{\max} \left(F_{\mathcal{G}, \sigma, T, a}^{N+k\tau}(\mathbf{x}), F_{\mathcal{G}, \sigma, T, a}^{k\tau}(\hat{\mathbf{x}}) \right) + d_{\max} \left(F_{\mathcal{G}, \sigma, T, a}^{k\tau}(\hat{\mathbf{x}}), \hat{\mathbf{y}} \right) < \frac{5a^k \varepsilon}{3},$$

for each $k \in \mathbb{N}$, which implies $\lim_{t \rightarrow \infty} \left| F_{\mathcal{G}, \sigma, T, a}^t(\mathbf{x}) - F_{\mathcal{G}, \sigma, T, a}^t(\mathbf{y}) \right| = 0$, where $\mathbf{y} = F_{\mathcal{G}, \sigma, T, a}^n(\hat{\mathbf{y}})$ with $n \equiv -N \pmod{\tau}$. It follows from here that $P(F_{\mathcal{G}, \sigma, a, T}, \mathbf{x}) = \tau$. In addition, since $\hat{\mathbf{y}} \in \text{closure} \left(\{F_{\mathcal{G}, \sigma, T, a}^t(\mathbf{x}) : t \in \mathbb{N}\}_{t \in \mathbb{N}} \right)$, then $\min_{0 \leq t < \tau} d_{\max} \left(F_{\mathcal{G}, \sigma, a, T}^t(\hat{\mathbf{y}}), \Delta_T \right) = \varepsilon$.

5.1.3. *The complement of $O_{a,V}$ has zero measure for $a < \max_{u \in V} (\text{Id}(u) + 1)^{-1}$.*

Fix \mathcal{G}, σ, a , and for $(T, \mathbf{x}) \notin O_{\mathcal{G}, \sigma, a}$ let $D^{(t)} := D_{\mathcal{G}, \sigma, a}(F_{\mathcal{G}, \sigma, T, a}^t(\mathbf{x}))$ for each $t \in \mathbb{N}$. Then, there exists a sequence $\{t_k \in \mathbb{N}\}_{k \in \mathbb{N}}$, and $u, v \in V$, such that

$$\begin{aligned} T_{(u,v)} &= \lim_{k \rightarrow \infty} \left(a^{t_k} \mathbf{x}_u + (1-a) \sum_{t=1}^{t_k} a^{t-1} D_u^{(t_k-t)} \right) \\ (12) \quad &= (1-a) \lim_{k \rightarrow \infty} \left(\sum_{t=1}^{t_k} a^{t-1} D_u^{(t_k-t)} \right). \end{aligned}$$

For each $\mathbf{x} \in [0, 1]^V$ fixed, define the fiber

$$(13) \quad C_{\mathcal{G}, \sigma, a}(\mathbf{x}) := \{T \in [0, 1]^A : (T, \mathbf{x}) \notin O_{\mathcal{G}, \sigma, a}\}.$$

Then, according to Equation (12) we have

$$C_{\mathcal{G}, \sigma, a}(\mathbf{x}) \subset \bigcup_{(u,v) \in A} \left\{ T \in [0, 1]^A : T_{(u,v)} \in \frac{1-a}{\text{Id}(u)} \times \text{closure}(\Omega_{\mathcal{G}, a, u}) \right\},$$

where

$$\Omega_{\mathcal{G}, a, u} := \bigcup_{N=1}^{\infty} \left\{ \sum_{s=0}^{N-1} a^s \mathbf{k}_s : (\mathbf{k}_s)_{s=0}^{N-1} \in \{0, 1, \dots, \text{Id}(u)\}^N \right\}.$$

If $a < (\text{Id}(u) + 1)^{-1}$ for some $u \in V$, then $\text{closure}(\Omega_{\mathcal{G}, a, u})$ is a Cantor set of dimension $\log(\text{Id}(u) + 1) / \log(1/a) < 1$. Hence, Fubini's Theorem implies, for $a < \max_{v \in V} (\text{Id}(u) + 1)^{-1}$, that the fiber $C_{\mathcal{G}, \sigma, a}(\mathbf{x})$ has zero $\#A$ -dimensional volume for each $\mathbf{x} \in [0, 1]^V$.

5.1.4. *The complement of $O_{a,V}$ has zero measure for $a \geq \max_{u \in V} (\text{Id}(u) + 1)^{-1}$.*

The fact that $\text{vol}(C_{\mathcal{G},\sigma,a}(\mathbf{x})) = 0$ for each $\mathbf{x} \in [0,1]^A$ and arbitrary $a \in (0,1)$, derives from a result by Kruglikov and Rypdal. Theorem 2 in [12] gives an upper bound for the topological entropy of the symbolic system associated to a non-degenerated piecewise affine map. The upper bound is related to the exponential rate of angular expansion under the action of the map. For piecewise affine conformal maps, which is the case of discrete-time regulatory networks, this upper bound vanishes. Hence, Kruglikov and Rypdal's theorem directly applies to our case, implying that

$$(14) \quad \limsup_{N \rightarrow \infty} \frac{\log \# \mathcal{L}_{(T,\mathbf{x},u)}^{(N)}}{N} = 0,$$

where for each \mathcal{G}, σ , and a fixed,

$$\mathcal{L}_{(T,\mathbf{x},u)}^{(N)} := \left\{ (\mathbf{k}_{t+s})_{s=0}^{N-1} \in \{0,1,\dots,\text{Id}(u)\}^N : D_{\mathcal{G},\sigma,T}(F_{\mathcal{G},\sigma,T,a}^t(\mathbf{x}))_u = \frac{\mathbf{k}_t}{\text{Id}(u)} \ \forall t \in \mathbb{N} \right\}.$$

Therefore, for each T , there exists $N = N(T, \mathbf{x}, u) \in \mathbb{N}$ such that $\# \mathcal{L}_{(T,\mathbf{x},u)}^{(N)} \leq ((1+a)/2a)^N$. Fix $u \in V$, and for each $N \in \mathbb{N}$ and $\mathcal{D} \subset \{0,1,\dots,\text{Id}(u)\}^N$, define

$$\mathcal{T}_{\mathcal{D}} := \left\{ x = \sum_{t=0}^{\infty} a^t \mathbf{k}_t : (\mathbf{k}_{(k+1)N-1}, \dots, \mathbf{k}_{kN}) \in \mathcal{D} \ \forall k \geq 0 \right\}.$$

With this we have, for the fiber $C_{\mathcal{G},\sigma,a}(\mathbf{x})$ defined in (13), the inclusion

$$(15) \quad C_{\mathcal{G},\sigma,a}(\mathbf{x}) \subset \bigcup_{(u,v) \in A} \bigcup_{N \in \mathbb{N}} \bigcup_{\substack{\mathcal{D} \subset \{0,1,\dots,\text{Id}(u)\}^N \\ \#\mathcal{D} \leq ((1+a)/2a)^N}} \left\{ T \in [0,1]^A : T_{(u,v)} \in \frac{1-a}{\text{Id}(u)} \times \text{closure}(\mathcal{T}_{\mathcal{D}}) \right\}.$$

Now, for each $m \in \mathbb{N}$, a prefix $\mathbf{k} \in \left(\mathcal{L}_{(T,\mathbf{x},u)}^{(N)} \right)^m$ defines an interval

$$I_{\mathbf{k}} := \left\{ x = \sum_{t=0}^{\infty} \omega_t a^t : (\omega_t)_{t=0}^{mN-1} = (\mathbf{k}_{mN-t})_{t=1}^{mN} \right\},$$

and we have

$$\text{closure}(\mathcal{T}_{\mathcal{D}}) = \bigcap_{m=1}^{\infty} \left(\bigcup_{\mathbf{k} \in \mathcal{D}^m} \text{closure}(I_{\mathbf{k}}) \right).$$

Since $\text{vol}(I_{\mathbf{k}}) = \text{vol}(\text{closure}(I_{\mathbf{k}})) = \text{Id}(u) a^{mN} / (1-a)$ for each $\mathbf{k} \in \left(\mathcal{L}_{(T,\mathbf{x},u)}^{(N)} \right)^m$, then

$$\text{vol}(\text{closure}(\mathcal{T}_{\mathcal{D}})) \leq (\#\mathcal{D})^m a^{mN} \frac{\text{Id}(u)}{1-a},$$

for each $m \in \mathbb{N}$. Hence, $\text{vol}(\text{closure}(\mathcal{T}_{\mathcal{D}})) = 0$ for each $\mathcal{D} \subset \{0,1,\dots,\text{Id}(u)\}^N$ such that $\#\mathcal{D} \leq ((1+a)/2a)^N$. Taking into account (15), Fubini's Theorem implies, that the fiber $C_{\mathcal{G},\sigma,a}(\mathbf{x})$ has zero $\#A$ -dimensional volume for each $\mathbf{x} \in [0,1]^V$.

Using once again Fubini's, we finally conclude,

$$\mathbb{P}_{a,\eta}(\mathcal{F}_{a,V} \times [0,1]^V \setminus O_{a,V}) \leq \sum_{\mathcal{G} \in \mathfrak{G}_V} \sum_{\sigma \in \{-1,1\}^A} \mathbb{P}_G(\mathcal{G}) \mathbb{P}_{A,\eta} \sigma \int_{\mathbf{x} \in [0,1]^V} \text{vol}(C_{\mathcal{G},\sigma,a}(\mathbf{x})) \, d\mathbf{x} = 0.$$

□

Remark 1. In the statement of Theorem 1 we can replace the probability measure $\mathbb{P}_{a,\eta}$ by any other Borel measure \mathbb{P} in $\mathcal{F}_{a,V} \times [0,1]^V$ such that, for each $\mathcal{G} \in \mathfrak{G}_V, \sigma \in \{-1,1\}^A$, and $\mathbf{x} \in [0,1]^V$ fixed, the $\#A$ -dimensional projection

$$\mathbb{P}_T(\mathcal{J}) := \mathbb{P}\{(F_{\mathcal{G},\sigma,T,a}, \mathbf{x}) \in \mathcal{F}_{a,V} \times [0,1]^V : T \in \mathcal{J}\}$$

is absolutely continuous with respect to the Lebesgue measure.

Remark 2. From the arguments developed in Paragraph 5.1.3, it follows that for $a < \min_{u \in V} (\text{Id}(u) + 1)^{-1}$, the set $O_{\mathcal{G},\sigma,a}$ defined in (10) is open and dense. This ensures that orbits are generically uniformly far from the discontinuity set. As a consequence, periodic attractors not intersecting the discontinuity set are generic for $a < \min_{u \in V} (\text{Id}(u) + 1)^{-1}$. On the other hand, the argument in Paragraph 5.1.4 ensures, as long as we consider distributions absolutely continuous with respect to Lebesgue for thresholds, that orbits are almost surely uniformly far from the discontinuity set. Hence, in the general case, almost all initial conditions converge to periodic attractors not intersecting the discontinuity set.

5.2. Proof of Theorem 2.

This theorem consist of two claims. The first one establishes the stability of the oscillatory subnetworks, while the second one gives the equivalence between the dynamics restricted to that subnetwork and the dynamics supported by the subnetwork considered as an isolated system. Both claims follow from direct computations.

5.2.1. Stability of the oscillatory subnetworks.

Since $\mathbb{P}_{a,\eta}(\mathcal{G}_{\text{osc}} = \bar{\mathcal{G}}) > 0$, then, there exists $\mathcal{G} \in \mathfrak{G}_V, \sigma \in \{-1,1\}^A$, and $(\tilde{T}, \tilde{\mathbf{x}}) \in O_{\mathcal{G},\sigma,a}$, such that $\mathcal{G}_{\text{osc}}(F_{\mathcal{G},\sigma,\tilde{T},a}, \tilde{\mathbf{x}}) = \bar{\mathcal{G}}$. As proved in Paragraph 5.1.2, there exists $0 < \varepsilon < 1/2$, $\tau \in \mathbb{N}$, and $\tilde{\mathbf{y}} \in \text{Per}_\tau(F_{\mathcal{G},\sigma,\tilde{T},a})$, such that $\lim_{t \rightarrow \infty} |F_{\mathcal{G},\sigma,\tilde{T},a}^t(\tilde{\mathbf{x}}) - F_{\mathcal{G},\sigma,\tilde{T},a}^t(\tilde{\mathbf{y}})| = 0$ and

$$\inf_{t \geq 0} d_{\max} \left(F_{\mathcal{G},\sigma,\tilde{T},a}^t(\tilde{\mathbf{x}}), \Delta_{\tilde{T}} \right) = \min_{0 \leq t < \tau} d_{\max} \left(F_{\mathcal{G},\sigma,\tilde{T},a}^t(\tilde{\mathbf{y}}), \Delta_{\tilde{T}} \right) = 2\varepsilon.$$

From this it readily follows that $\mathcal{G}_{\text{osc}}(F_{\mathcal{G},\sigma,T,a}, \mathbf{y}) = \bar{\mathcal{G}}$ for each $(T, \mathbf{y}) \in B_\varepsilon(\tilde{T}) \times B_\varepsilon(\tilde{\mathbf{y}})$.

Let us now extend \mathcal{G} , σ , and \tilde{T} , and redefine $\tilde{\mathbf{y}}$ at each vertex $v \in \bar{V}$ such that $\text{Id}_{\text{osc}}(v) = \text{Id}(v)$ (remind that $\text{Id}_{\text{osc}}(v) := \#\{u \in V : (u,v) \in \bar{A} \equiv A_{\text{osc}}\}$). Choose $u \notin \bar{V}$, and include the arrow (u,v) in A . Then, if $\tilde{\mathbf{y}}_u < 1 - 2\varepsilon$, define $\sigma_{(u,v)} = 1$ and $\tilde{T}_{(u,v)} = 1 - \varepsilon$. Otherwise, if $\tilde{\mathbf{y}}_u > 2\varepsilon$, make $\sigma_{(u,v)} = -1$ and $\tilde{T}_{(u,v)} = \varepsilon$. Finally, redefine $\tilde{\mathbf{y}}_v = \text{Id}(v) \tilde{\mathbf{y}}_v / (\text{Id}(v) + 1) + 1/(\text{Id}(v) + 1)$ at that vertex. A simple computation shows that, in the redefined system, $\mathcal{G}_{\text{osc}}(F_{\mathcal{G},\sigma,T,a}, \mathbf{y}) = \bar{\mathcal{G}}$, for each $(T, \mathbf{y}) \in B_\varepsilon(\tilde{T}) \times B_\varepsilon(\tilde{\mathbf{y}})$. Therefore, taking into account that

by hypothesis $\mathbb{P}_G(\mathcal{G}) > 0$ for all $\mathcal{G} \in \mathfrak{G}_V$, we can assume without loss of generality that $\text{Id}_{\text{osc}}(v) < \text{Id}(v)$ for all $v \in \bar{V}$.

By definition, if $(u, v) \in A \setminus \bar{A}$ then $\theta_{(u,v)} := H(\bar{\sigma}_{(u,v)}(\tilde{\mathbf{y}}_u^t - \tilde{T}_{(u,v)}))$ remains constant in time, as well as $D(v) := \sum_{(v,u) \in A \setminus \bar{A}} \theta_{(v,u)}$ for each $v \in V$. Let us now modify σ and \bar{T} for the arrows leaving $\bar{\mathcal{G}}$. For $u \in \bar{V}$, and each $v \notin \bar{V}$, if $D(u) > 0$, make $\tilde{T}_{(u,v)} \mapsto \tilde{T}_{(u,v)} \times D(u)/\text{Id}(u)$, and

$$\sigma_{(u,v)} \mapsto \begin{cases} \sigma_{(u,v)} & \text{if } \theta_{(u,v)} + \sigma_{(u,v)} \in \{-1, 2\} \\ -\sigma_{(u,v)} & \text{if } \theta_{(u,v)} + \sigma_{(u,v)} \in \{0, 1\}. \end{cases}$$

Otherwise, if $D(u) = 0$, then $\tilde{T}_{(u,v)} \mapsto \tilde{T}_{(u,v)} \times (\text{Id}(u) - \text{Id}_{\text{osc}}(u))/\text{Id}(u) + \text{Id}_{\text{osc}}(u)/\text{Id}(u)$, and

$$\sigma_{(u,v)} \mapsto \begin{cases} -\sigma_{(u,v)} & \text{if } \theta_{(u,v)} + \sigma_{(u,v)} \in \{-1, 2\} \\ \sigma_{(u,v)} & \text{if } \theta_{(u,v)} + \sigma_{(u,v)} \in \{0, 1\}. \end{cases}$$

This modification in σ and \bar{T} uncouples the dynamics on \bar{V} from that on $V \setminus \bar{V}$, so that now we can set $\sigma|_{\bar{A}} \equiv \bar{\sigma}$ for arbitrary $\bar{\sigma} \in \{-1, 1\}^{\bar{A}}$. In this way we obtain a digraph extension $\bar{\mathcal{G}}_{\text{ext}} := \mathcal{G} \supset \bar{\mathcal{G}}$, and for each $\bar{\sigma} \in \{-1, 1\}^{\bar{A}}$ an extension $\bar{\sigma}_{\text{ext}} := \sigma \in \{-1, 1\}^A$ with $\bar{\sigma}_{\text{ext}}|_{\bar{A}} = \bar{\sigma}$. For any of these extensions, a direct computation shows that $\lim_{t \rightarrow \infty} F_{\bar{\mathcal{G}}_{\text{ext}}, \bar{\sigma}_{\text{ext}}, T, a}^t(\mathbf{x})_v = D(v)/\text{Id}(v) = \bar{\mathbf{y}}_v$ for $v \notin \bar{V}$, and $F_{\bar{\mathcal{G}}_{\text{ext}}, \bar{\sigma}_{\text{ext}}, T, a}^t(\mathbf{x})_v \in [D(v)/\text{Id}(v), (D(v) + \text{Id}_{\text{osc}}(v))/\text{Id}(v)]$, for all $t \geq 0$ and $v \in \bar{V}$, whenever

$$\mathbf{x} \in \bar{\mathcal{J}} \times \mathcal{J}' := \left(\prod_{v \notin \bar{V}} [\tilde{\mathbf{y}}_v - \varepsilon, \tilde{\mathbf{y}}_v + \varepsilon] \cap [0, 1] \right) \times \left(\prod_{v \in \bar{V}} \left[\frac{D(v)}{\text{Id}(v)}, \frac{D(v) + \text{Id}_{\text{osc}}(v)}{\text{Id}(v)} \right] \right),$$

and

$$T \in \bar{\mathcal{I}} \times \mathcal{I}' := \left(\prod_{(u,v) \in A \setminus \bar{A}} [\tilde{T}_{(u,v)} - \varepsilon, \tilde{T}_{(u,v)} + \varepsilon] \cap [0, 1] \right) \times \left(\prod_{(u,v) \in \bar{A}} \left[\frac{D(u)}{\text{Id}(u)}, \frac{D(u) + \text{Id}_{\text{osc}}(u)}{\text{Id}(u)} \right] \right).$$

Therefore, $\mathcal{G}_{\text{osc}}(F_{\bar{\mathcal{G}}_{\text{ext}}, \bar{\sigma}_{\text{ext}}, T, a}^t, \mathbf{x}) \subseteq \bar{\mathcal{G}}$ for each $(T, \mathbf{x}) \in \bar{\mathcal{I}} \times \mathcal{I}' \times (\bar{\mathcal{J}} \times \mathcal{J}')$, and $\bar{\sigma} \in \{-1, 1\}^{\bar{A}}$.

5.2.2. Equivalence to the subnetwork considered as an isolated system.

We will use the same notation as in Subsubsection 5.2.1. Let $\sigma := \bar{\sigma}_{\text{ext}}$, and each $(T, \mathbf{x}) \in (\bar{\mathcal{I}} \times \mathcal{I}') \times (\bar{\mathcal{J}} \times \mathcal{J}')$, and $t \in \mathbb{N}$, let $\mathbf{x}^t := F_{\bar{\mathcal{G}}_{\text{ext}}, \bar{\sigma}_{\text{ext}}, T, a}^t(\mathbf{x})$. For each $v \in V$, the term

$$D(v) := \sum_{(u,v) \in A \setminus \bar{A}} H(\sigma_{(u,v)}(\mathbf{x}_u^t - T_{(u,v)})) = \sum_{(u,v) \in A \setminus \bar{A}} H(\sigma_{(u,v)}(F_{\bar{\mathcal{G}}, \sigma, \bar{T}, a}^t(\tilde{\mathbf{y}})_u - \tilde{T}_{(u,v)})),$$

remains constant in time. Since $\sigma|_{\bar{A}} \equiv \bar{\sigma}$,

$$\mathbf{x}_v^{t+1} = a\mathbf{x}_v^t + \frac{\text{Id}_{\text{osc}}(v)}{\text{Id}(v)} \left(\frac{(1-a)}{\text{Id}_{\text{osc}}(v)} \sum_{(u,v) \in \bar{A}} H(\bar{\sigma}_{(u,v)}(\mathbf{x}_u^t - T_{(u,v)})) \right) + (1-a) \frac{D(v)}{\text{Id}(v)},$$

which can be rewritten as

$$(16) \quad \Phi_V(\mathbf{x}^{t+1})_v = a\Phi_V(\mathbf{x}^t)_v + \frac{1-a}{\text{Id}_{\text{osc}}(v)} \sum_{(u,v) \in \bar{A}} H(\bar{\sigma}_{(u,v)}(\Phi_V(\mathbf{x}^t)_u - \Phi_A(T)_{(u,v)})),$$

where $\Phi_A : \bar{\mathcal{I}} \times \mathcal{I}' \rightarrow [0, 1]^{\bar{A}}$ and $\Phi_V : \bar{\mathcal{J}} \times \mathcal{J}' \rightarrow [0, 1]^{\bar{V}}$ are affine transformations defined as follows. We have $\Phi_A(\bar{T} \times T') = \mathcal{D}_{\bar{A}}\bar{T} + \mathcal{C}_{\bar{A}}$, with

$$(\mathcal{D}_{\bar{A}}\bar{T})_{(u,v)} = \frac{\text{Id}(u)}{\text{Id}_{\text{osc}}(u)} \times \bar{T}_{(u,v)}, \quad \text{and} \quad (\mathcal{C}_{\bar{A}})_{(u,v)} = -\frac{D(u)}{\text{Id}_{\text{osc}}(u)},$$

for each $(u, v) \in \bar{A}$, and $\Phi_V(\bar{\mathbf{x}} \times \mathbf{x}') = \mathcal{D}_{\bar{V}}\bar{\mathbf{x}} + \mathcal{C}_{\bar{V}}$, with

$$(\mathcal{D}_{\bar{V}}\bar{\mathbf{x}})_u = \frac{\text{Id}(v)}{\text{Id}_{\text{osc}}(v)} \times \bar{\mathbf{x}}_v, \quad \text{and} \quad (\mathcal{C}_{\bar{V}})_v = -\frac{D(v)}{\text{Id}_{\text{osc}}(v)},$$

for each $v \in \bar{V}$. The result follows from Equation (16), which establishes

$$F_{\bar{\mathcal{G}}, \bar{\sigma}, \Phi_A(T), a}(\Phi_V(\mathbf{x})) = \Phi_V(F_{\bar{\mathcal{G}}_{\text{ext}}, \bar{\sigma}_{\text{ext}}, T, a}(\mathbf{x}))$$

for all $(T, \mathbf{x}) \in \mathcal{I} \times \mathcal{J}$, and from the fact that Φ_A and Φ_V are affine and surjective. \square

Remark 3. In the statement of Theorem 2, instead of the hypothesis $\mathbb{P}_G(\mathcal{G}) > 0$ for all $\mathcal{G} \in \mathfrak{G}_V$, we could have directly supposed that the oscillatory subnetwork $\bar{\mathcal{G}} := (\bar{V}, \bar{A})$ is such that $\text{Id}_{\text{osc}}(v) < \text{Id}(v)$ for each $v \in \bar{V}$. By assuming this, we avoid the condition $\bar{V} \subsetneq V$ as well. This alternative formulation allows us to consider the emergence of modularity in Barabási–Albert random networks, for which $\mathbb{P}_{\text{BA}}(\mathcal{G}) = 0$ for some digraphs $\mathcal{G} \in \mathfrak{G}_V$.

6. FINAL COMMENTS AND CONCLUSIONS

From our point of view, one of the most important theoretical problem in regulatory dynamics concerns the relations between the structure of the underlying network and the possible dynamical behaviors the system generates. We have already established bounds relating the structure of the underlying network, and the growth of distinguishable orbits [16]. Here, following [22], we have considered regulatory networks with interactions and initial conditions chosen at random at the beginning of the evolution. Within this approach, individual orbits become elements in a sample space, and the characteristics of the asymptotic behavior can be considered as orbit dependent random variables. The structure of the underlying network, random in this approach, is encoded in a probability distribution over a set of directed graphs. In two interesting cases we have explored, the asymptotic oscillations concentrates on a relatively small subnetwork, whose structure depends on both the proportion of inhibitory interactions, and the contraction rate. We have proved that the dynamics observed on this subnetwork is equivalent to the dynamics supported by the subnetwork considered as an isolated system. We interpret this as the emergence of modularity. Modularity allows us to predict asymptotic periods in regulatory networks admitting disconnected oscillatory subnetworks.

We want to remark Theorem 1, which has important technical implications. It ensures, as long as we consider distributions absolutely continuous with respect to Lebesgue for thresholds and initial conditions, that a random orbit converges to a periodic attractor. Furthermore, this periodic attractor does not intersect the discontinuity set. We have also proved, in the case of small contraction rates, that the periodic attractors are generic. This can be deduced from the argument in Paragraph 5.1.3.

As mentioned above, in order to determine the distribution of the asymptotic period, and the characteristics of the oscillatory subnetwork, a detailed numerical study of the examples presented in Section 4 is required. Heuristic computations could guide those numerical studies, and it is our intention to proceed in this direction in a subsequent work.

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